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How pulse disturbances shape size-abundance pyramids

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Abstract

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INTRODUCTION

Ecological pyramids, which represent the distribution of abundance and biomass of organisms across body-sizes or trophic levels, reveal one of the most striking regularities among communities (Elton 1927; Lindeman 1942; Trebilco *et al.* 2013). Several types of pyramids have been reported in ecological research, as well as distinct underlying mechanisms to explain their shape. For example, trophic pyramids describe the distribution of abundance or biomass along discrete trophic levels (Fig. 1a). The inefficiency in energy transfer from resources to consumers as well as strong self-regulation within trophic levels provide the main explanation for their shape (Lindeman 1942; Barbier & Loreau 2019). Alternatively, size-abundance pyramids (Fig. 1b,c), also known as the pyramid of numbers (Elton 1927), the Damuth law (Damuth 1981), or the abundance size spectrum (Sprules & Barth 2016), describe the distribution of abundance across body-sizes

and can be studied both within and across trophic guilds (Elton 1927; Trebilco *et al.* 2013). The energetic equivalence rule, along with the metabolic theory of ecology, provide theoretical expectations regarding the shape of such size-abundance pyramids: in a community where all individuals feed on a common resource (i.e. within a trophic group), population abundance should be proportional to $M^{-0.75}$, where M is body-size, and biomass should be proportional to $M^{0.25}$ (Damuth 1981; Brown *et al.* 2004; White *et al.* 2007).

As with most concepts in ecology, these relationships correspond to theoretical baselines that are predicted under steady-state conditions, which are rarely met in nature (DeAngelis & Waterhouse 1987; Hastings 2004, 2010). Most natural ecosystems and communities are exposed to a wide range of environmental fluctuations and disturbances, ranging from harvesting to extreme weather events. Furthermore, many of these disturbances are expected to increase in frequency and intensity in the context of global change, as illustrated by recent large scale wildfires, floods or hurricanes (Coumou & Rahmstorf 2012; Hughes *et al.* 2017; Harris *et al.* 2018). Such disturbances increase population mortality and could trigger even faster changes in community structure and dynamics than gradual changes in average conditions (Jentsch *et al.* 2009; Wernberg *et al.* 2013; Woodward *et al.* 2016).

Despite the extensive literature on disturbance ecology (Sousa 1984; Yodzis 1988; Petraitis *et al.* 1989; Fox 2013; Dantas *et al.* 2016; Thom & Seidl 2016), the effects of disturbances on community structure and biomass distribution remain poorly understood (Donohue *et al.* 2016). On the one hand, ecologists have often focused on the consequences of environmental disturbances on species richness (Huston 1979; Haddad *et al.* 2008; Bongers *et al.* 2009) and the coexistence of competing species (Violle *et al.* 2010; Miller *et al.* 2011; Fox 2013), rather than on body-size and biomass distribution (but see Woodward *et al.* (2016)). As such, the specific identity of species resistant (or not) to disturbances has received ample attention, with various definitions of

disturbance-resistant species groups (Sousa 1980, 1984; Lavorel *et al.* 1997). These studies have pointed out key demographic traits, notably population growth rate and carrying capacity, that determine species' capacities to persist in a disturbed environment (McGill *et al.* 2006; Haddad *et al.* 2008; Enquist *et al.* 2015; Woodward *et al.* 2016). On the other hand, the metabolic theory of ecology uses the scaling of metabolic rate with body-size to predict a set of structural and functional characteristics across biological scales (Brown *et al.* 2004). At the community level, it demonstrates how size-abundance pyramids emerge from the scaling of population growth rate and abundance with body-size (Trebilco *et al.* 2013). Surprisingly, a formal integration of the theory on disturbances with the metabolic theory of ecology is still lacking, but would allow ecologists to generalize and predict the effect of environmental disturbances on the shape of size-abundance pyramids.

Here, we integrate these two disconnected fields by developing a size-based model for population persistence, assuming that the scaling of population growth rate with body-size is the leading mechanism determining the response of size-abundance pyramids to disturbances. We predict the shape of size-abundance pyramids within a trophic guild in response to repeated pulse disturbances of varying frequency and intensity affecting all species in a similar way, regardless of their size. Such disturbances represent a wide range of environmental pressures that increase species mortality, such as floods, wildfires, or hurricanes. They differ from the disturbance studies developed in fishery sciences, that specifically addressed the effect of a press, size-selective disturbance (i.e. fishing) on the abundance size spectrum (Jennings *et al.* 2002; Shin *et al.* 2005; Petchey & Belgrano 2010; Sprules & Barth 2016). We then experimentally test the predicted responses of size-abundance pyramids and standing biomass to disturbances, using microbial communities composed of aquatic species with body-sizes and populations densities varying over

several orders of magnitudes. We finally discuss the general implications of our findings for the structure and functioning of communities exposed to environmental disturbances.

MATERIALS AND METHODS

A model for size-abundance pyramids exposed to disturbances

We build a mechanistic model to predict how disturbance frequency and intensity modulate the shape of size-abundance pyramids and community total biomass. We describe the dynamics of population abundance N with a logistic model:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \quad (1)$$

where r is population growth rate and K is population carrying capacity. We model a disturbance regime, corresponding to a recurrent abundance reduction, of intensity I (fraction of abundance) and frequency f or period $T=1/f$ (time between two disturbances, Fig. 2a). We can demonstrate that a population persists in a disturbed environment only if its growth rate balances the long-term effect of the disturbance regime (adapted from Harvey *et al.* 2016), that is:

$$r > -\frac{\ln(1-I)}{T} \quad (2)$$

From equation (2), we can predict the set of disturbance regimes a population can sustain according to its growth rate (Fig. 2b), as well as the minimum generation time ($1/r$) needed to maintain a viable population (Fig. S1). We then use the allometric relationship between population growth rate r and average body-size M, that is $r = c \times M^a$ with $a = -¼$ (Brown *et al.* 2004; Savage *et al.* 2004) and c a positive constant, to derive the following size-specific criterion for population persistence under a disturbance regime:

$$M \leq \left(\frac{\ln(1-I)}{T \times c}\right)^{-4} \quad (3)$$

Equation (3) indicates that a species can persist in a disturbed environment only if its average body-size is below a certain value. Note that this analytical criterion is applicable to any biological and temporal scale. Indeed, the disturbance frequency and population growth rate are expressed with the same time unit and can range from hours (e.g. fast-growing microbial organisms) to years (e.g. slow-growing organisms such as large mammals). To investigate the effect of disturbances on the shape of size-abundance pyramids, we derive the mean abundance at dynamical equilibrium $\bar{N}$ of a population under a given disturbance regime (i.e. averaged over a time period, see Appendix 1 for detailed steps), that is:

$$\bar{N} = K\left(\frac{ln(1-I)}{T \times r} + 1\right) \quad (4)$$

where K corresponds to the carrying capacity of the population, which also scales with body-size on a logarithmic scale (Brown & Gillooly 2003; Brown *et al.* 2004): $ln(K) = a_K \ln(M) + b_K$, where a_K and b_K are normalizing constants. We use this allometric relationship to express mean abundance as a function of mean population body-size and finally obtain:

$$ln(\bar{N}) = a_K \ln(M) + b_K + ln\left(\frac{ln(1-I)}{T e^{a_r \ln(M) + b_r}} + 1\right) \quad (5)$$

The formula is valid when the expression in parentheses in the right-hand term is positive, which corresponds to the persistence criteria given in equations (2) and (3). We express population biomass, B, as the product of mean abundance at dynamical equilibrium, $\bar{N}$, and the average individual body-size in the population, M, that is $B = \bar{N}M$.

We extend this approach to multispecies assemblages composed of potentially hundreds of co-occurring species with different body-sizes (see detailed method in Appendix 2 and Table S1 for parameter values). We assume that all species' populations follow a logistic growth and are constrained by intraspecific competition only (an assumption relaxed in Appendix 3). From equation (3) and (5), we expect that disturbances will decrease the maximum size observed in the

117 community as well as total biomass. We use this analytical approach to explore how community
118 size-structure, a more tractable representation of abundance distribution across size-classes
119 compared to pyramids (Fig. 1b), and total community biomass will respond to a whole landscape
120 of disturbance frequencies and intensities (Fig. 3).
121
122 **Disturbance experiment on microbial communities**
123 We conducted an experiment in aquatic microcosms inoculated with 13 protist species and
124 a set of common freshwater bacteria as a food resource. The protist species cover a wide range of
125 body-sizes (from 10–10^3 µm) and densities (10–10^5 individuals/ml, Giometto *et al.* 2013). General
126 lab procedures follow the protocols described in Altermatt *et al.* (2015), and build upon previous
127 work on pulsed disturbance effects on diversity (Altermatt et al., 2011; Harvey et al. 2016) and
128 invasion dynamics (Mächler & Altermatt, 2012). Detailed microcosm description and set-up are
129 presented in Appendix 4. In short, we performed a factorial experiment in which we varied
130 disturbance frequency and intensity, resulting in a total of twenty different disturbance regimes.
131 Disturbance was achieved by boiling a subsampled fraction of the well-mixed community in a
132 microwave so that all species experience the same level of density reduction. All protists were
133 killed by the microwaving process. We let the medium cool down before putting it back into the
134 microcosm. We disturbed microcosms at five intensities: 10, 30, 50, 70 and 90 % and at four
135 frequencies: $f = 0.08, 0.11, 0.16$ and 0.33, corresponding to a disturbance every 12, 9, 6 and 3 days,
136 respectively. The experiment lasted for 21 days, or about 10–50 generations depending on species.
137 Each disturbance regime was replicated six times. To control for the intrinsic variability of
138 community size-structure, we cultured eight undisturbed microcosms under the same conditions.
139 We sampled 0.2 ml of each microcosm daily to quantify individual body-sizes (i.e. cell area in
140 μm^2), protist abundances (individuals/µl) and total community biomass (i.e. total bioarea in

141 $\mu m^2/\mu l$) using a standardized video procedure (Altermatt *et al.* 2015; Pennekamp et al. 2017). We
142 binned the observed individuals into twelve size-classes ranging from 0 to 1.6×10^5 μm^2 in order to
143 get statistically comparable community size-structures. Mean protist abundance and its standard
144 deviation in each size-class were calculated over 21 time points and 6 replicates (total of 126
145 observations) for each treatment and over 21 time points and 8 replicates (total of 168 observations)
146 for the control communities. We performed Welch two sample t-tests of mean comparison
147 (treatment versus control) to determine which disturbance regime had a significant effect on
148 community size-structure and total community biomass (Table S2).
149
150 **Model parameterization**
151 We parameterized the model using the experimental data in order to test the capacity of the model
152 to predict the effect of a given disturbance regime on the size-structure of real communities. The
153 model required the following input parameters: the carrying capacities of each size-class as well as
154 the slope and the intercept of the allometric relationship between growth rate and body-size. We
155 took the average abundances of the undisturbed communities (8 controls) to the estimate carrying
156 capacities in each size-class. We fitted a logistic growth model to the recovery dynamics of each
157 size-class after one disturbance (I = 90%) to obtain growth rate estimations. Specifically, we used
158 the data from the treatment $\{I=90\%, f=0.08\}$ (i.e. highest intensity, lowest frequency) to estimate
159 the parameters of a logistic growth model over 12 time points using the function *nls*() of the *stats*
160 package in R (R Core Team 2019). We determined the relationship between growth rate and body-
161 size in our experimental communities using the 13 time-series (covering 6 size-classes) that
162 displayed a logistic growth. We obtained the following allometric relationship: $ln(r) =$
163 $-0.37 \times \ln(M) + 3.75$ (p-value = 0.005, R^2 = 0.47). Using this parameterization, we produced

164 theoretical predictions on the size-abundance pyramids expected in the experimental disturbance
165 regimes. We then quantitively compared these predictions with the size-abundance pyramids
166 observed in the experimental communities. We performed ordinary least-squares regressions to
167 characterize the relationship between observed and predicted log-transformed mean abundances
168 among size-classes for all the disturbance regimes.
169
170 **RESULTS**
171 **Model predictions**
172 We first explore the effects of increasing disturbance frequency (Fig. 3a, c). Infrequent
173 disturbances do not strongly affect community size-structure and only decrease the mean
174 abundance of the largest size-classes (Fig. 3a, $f = 0.1$ in dark blue). Maximum body-size gradually
175 decreases as disturbance frequency increases, corresponding to the extinction of large, slow-
176 growing species (Fig. 3a, $f = 0.25$ in light blue). Disturbance frequency also affects the community
177 size-structure through its effect on mean abundance. For frequent disturbance events, the mean
178 abundance of all size-class decreases (Fig. 3a, $f = 0.5$ and 1 in orange and red respectively). The
179 effect of disturbance frequency on community-size structure have direct consequences for
180 community-level properties: we indeed observe an approximately linear decrease in total
181 community biomass (log) along a gradient of disturbance frequency, followed by an abrupt collapse
182 of the community for extreme disturbance regimes (Fig. 3c).
183 We then investigate the effect of increasing disturbance intensity (Fig. 3b, d). Similarly,
184 low intensity disturbances marginally affect community size-structure (Fig. 3c, $I = 30\%$ in blue)
185 and increasing disturbance intensity decreases maximum body-size and population mean
186 abundance. (Fig. 3b). Interestingly, the effect of disturbance intensity on community total biomass
187 is clearly nonlinear (Fig. 3d). Low to intermediate disturbance intensities do not affect total biomass

when disturbance frequency is low (e.g. f = 0.1 or 0.25 in Fig. 3d). However, strong intensities affect all population abundances and trigger a sharp decrease in total biomass, culminating in a crash of the system (e.g. $\{I > 90\%, f = 0.25\}$ in Fig 3d).

Experimental results

We experimentally investigated the effect of disturbance frequency and intensity on the size-structure of microbial communities. For a fixed intensity (set to I = 90% in Fig. 4a, see Fig. S2 for other intensities), infrequent disturbances (i.e. f = 0.08 and f = 0.11) had a significant negative impact only on the mean abundance of intermediate size-classes (between exp(9.6) and exp(10.5) μm^2, Welch two sample t-tests: $t \geq 2.5$, p-values ≤ 0.009, Table S2). When disturbance frequency increased to f = 0.16, the mean abundance of the smallest size-class also decreased (t = 3, p-value = 0.01, Table S2). Finally, at even more frequent disturbances (f = 0.33), all size-classes were negatively impacted, except the smallest one (Fig 5a and Table S3). Overall, increasing disturbance frequency led to an abundance depletion at intermediate sizes compared to undisturbed control communities.

Similarly, for a fixed frequency (set to f = 0.33 in Fig. 4b, see Fig. S3 for other frequencies), a low disturbance intensity I = 10 % (Fig. 4b) only affected intermediate size-classes (between exp(10) and exp(10.5) μm^2, $t \geq 4.1$, p-values ≤ 0.001, Table S2). Disturbance intensities I = 30% and 50% had a negative effect on the mean abundance of larger size-classes (between exp(10) and exp(11) μm^2, $t \geq 3$, p-values ≤ 0.01, Table S2). Finally, intensities I = 70% and I = 90% had an impact on all size-classes, except the smallest size-class that were not negatively impacted by change in disturbance intensity (Fig. 4b, Table S2). Interestingly, the following disturbance regimes had a positive effect of on the mean abundance of the smallest size-class: $\{I = 30\%, f =$

0.33}, t = -5.9, p-value < 0.001, (Fig. 4b), as well as {I = *50%,* f = 0.16}, {I = *70%,* f = 0.16} and {I = *70%,* f = 0.11} (Table S2, Fig. S2 and S3).

At the community-level, total biomass gradually decreased with disturbance frequency as expected by theory (Fig. 4c). All frequencies had a significant negative effect on total biomass compared to controls ($t \geq 8$, p-value < 0.001, Fig 4c). Disturbance intensities I = 10% and 30% had no significant effects on total community biomass ($I_{10\%}$: t = 0.75, p-value = 0.48, $I_{30\%}$: t = 0.5, p-value = 0.63), while total biomass strongly decreased for intensities above I = 50% ($I_{50\%}$: t = 6.1, p-value < 0.001, $I_{70\%}$: t = 12.7, p-value < 0.001, $I_{90\%}$: t = 14.2, p-value < 0.001, Fig. 4d).

Observed versus predicted effect of disturbances on size-abundance pyramids

We then compared our experimental results with the predictions of the model parameterized for our freshwater microbial communities (Figure 5). The model predicted well the observed mean abundances relative to carrying capacity for all the disturbance regimes in most of the size-classes. The slope of the linear regression between observed and predicted log mean abundances, including all size-classes in all disturbance regimes (218 points), was very close to the 1:1 line, which indicates a very good fit (Figure 5a, linear regression: y = -0.04 + 0.96x, R^2 = 0.96, p-value < 0.001). Additionally, the intercept of the linear regression was not significantly different from zero (t = 1.42, p-value = 0.16). We illustrate in Figure 5b-d the similarities as well as the differences between the predicted and observed community size-structures for varying disturbance frequencies with a disturbance intensity fixed to I = 90% (other disturbance regimes are shown in Figs. S4-S5). Overall, the predicted community structures were very similar to the observed ones. The model, however, often underestimated the mean abundance in the smallest size-class (Figure 5d). Furthermore, as mentioned in the previous section, some disturbance regimes had a positive effect

234 of on the mean abundance of the smallest size-class, which cannot, by construction, be predicted
235 by our model.
236
237 **DISCUSSION**
238 Most theories in community ecology have been developed under the assumption of steady-
239 state conditions (Hastings 2010). Yet, most of the world's ecosystems – specifically ≥75% of
240 land/freshwater and 50% of marine systems – have been altered by human activities and are facing
241 disturbances that put them clearly outside of such a steady state (IPBES 2018). Thus, to meet the
242 societal demand for an ecological science able to predict how ecosystems will respond to global
243 change (Petchey *et al.* 2015; Urban *et al.* 2016), this assumption needs to be relaxed. The challenge
244 is to develop models that make quantitative predictions regarding the impact of fluctuating
245 environmental conditions on the structural and functional characteristics of biological systems.
246
247 **Consequences of the growth-size relationship for communities exposed to disturbances**
248 Here we provide a robust and simple approach for predicting the size-structure of
249 communities exposed to any combination of disturbance frequency and intensity affecting all
250 species in a similar way, regardless of their body-size. We combine theory on disturbances with
251 the metabolic theory of ecology and assume that the scaling of population growth rate with body-
252 size is the leading mechanism determining the response of size-abundance pyramids to
253 disturbances. The model makes an important advance over the steady-state predictions of the
254 metabolic theory of ecology as it links quantitatively the shape of a size-abundance pyramid to the
255 disturbance regime experienced by the community (Fig. 6a–b). Overall, increasing disturbance
256 frequency or intensity narrows the bases of size-abundance pyramids and lowers their height. This
257 corresponds to the extinction of the largest species and a general reduction of population mean

abundances in all size-classes. Hence, we demonstrate that even disturbances that are not size-selective and do not target large species have a higher impact on these large species than on the small species.

The model is applicable across all biological and temporal scales as population growth rate and disturbance frequency are expressed with the same time units. Equation (2) can also apply to populations that do not show a scaling relationship between growth rate and body-size and predicts which disturbance regimes a species can sustain, or not, based on its generation time (Figs. 2 and S1). Importantly, our results are not specific to repeated pulse disturbances but also hold for press disturbances, which will affect the shape of size-abundance pyramids in an equivalent way (see Appendix 1 for a mathematical demonstration).

Our model offers a different perspective on community responses to disturbances by exploring the effect of repeated pulse disturbances of varying frequency and intensity on community size structure. The majority of theoretical studies on community stability have focused on local stability, which examine community's response to small pulse disturbances around one single equilibrium (Donohue *et al.* 2016), reflecting the great interest for the so-called diversity-stability debate (May 1972; McCann 2000; Allesina & Tang 2012; Jacquet *et al.* 2016). Our approach goes beyond local stability measures at the vicinity of one single attractor and is applicable to any combination of disturbance frequency or intensity. It predicts which species, based on its growth rate, can persist or not and how the abundances of the remaining species will be affected by a whole gradient of disturbances.

Note that the model depends on a number of technical assumptions. First, we restricted our theoretical approach to disturbance regimes where pulse disturbances are applied at fixed intervals with a fixed intensity. This choice, though relatively simplistic, allowed us to mirror the disturbance regimes applied to the experimental communities. To generalize, we also performed simulations

where we added stochasticity in the frequency and intensity of the disturbance regime to test the sensitivity of the theoretical results to variability in the periodicity and intensity of disturbances (Appendix 2). Our results were qualitatively robust to the addition of noise around average values of disturbance frequency and intensity, which simply increased the negative effect of one given disturbance regime on the largest size-classes (Fig. S8). Second, we consider that the allometric parameters of the relationships between population growth rate, carrying capacity and body-size are the same for all species (i.e. same slopes and intercepts). We therefore performed sensitivity analyses of Equation (5) and demonstrate that our results are robust to variation in these allometric parameters (Appendix 2, Fig. S6-7).

Experimental test of the theory

The disturbance experiment on microbial communities showed some similarities but also some departures from the theoretical predictions (Figure 5b-d). As expected from the analytical model, total community biomass gradually decreased with disturbance frequency and in a more nonlinear way with disturbance intensity (Fig. 4c–d, and Fig. 3c–d for the theoretical predictions). Interestingly, it was the intermediate and not the largest size-classes that were the most sensitive to disturbances in the microbial community. We provide below two possible explanations for this observation. Most likely, the abundances of the largest size-class might be already too low, and therefore too close to the methodologically-defined detection threshold, in the control communities to observe a significant effect of the disturbances of these size-classes. Second, this might be explained by the duration of the experiment (21 days), which was not long enough to capture the extinction of the largest species. We estimated the time to reach the dynamical equilibrium in the experiment with the model parameterized with experimental data (see Table S3). The model predicted that equilibrium is reached by the end of the experiment (21 days) for the size-classes

considered in all disturbance regimes but the strongest. With the highest frequency and intensity {I=90%; f=0.33} the equilibrium is reached by the three smallest size-classes (in 12, 18, and 21 days respectively).

Additionally, some combinations of disturbance frequency and intensity had a positive effect on the smallest size-class of microbes compared to controls, which corresponded to the main departure from the theoretical predictions (Figure 4a-b and Figure 5d). This could be explained by a disruption of biotic interactions (predation or competition) following a disturbance, allowing the remaining small species to grow in higher densities in the absence of other species (Cox & Ricklefs 1977; Ritchie & Johnson 2009; Bolnick *et al.* 2010). Such "interaction-release" mechanism could not be captured by our model of co-occurring species. We discuss below how interspecific interactions, such as competition, predation or parasitism, could modulate the shape of size-abundance pyramids exposed to disturbances.

Extending the model to communities of interacting species

To observe an "interaction-release" effect that will widen the pyramid's base, two conditions are required (but not sufficient): (i) the existence of a significant mismatch between the growth rates of the two interacting species, leading to differential response to disturbances, and (ii) the species with the slowest growth rate has a negative effect on the other species (i.e. predator, competitor or parasite). The latter condition seems unlikely for parasitism. For competitive interactions, a "competition-release" effect can potentially increase the abundance of small, fast-growing species that will recover faster from a disturbance event compared to larger competitors (e.g. Xi *et al.* (2019)). Finally, the existence of a "predation-release" effect is very likely as predators are generally larger than their prey and have slower growth rates (Brose *et al.* 2006, 2016; Barnes *et al.* 2010). In an additional analysis, we performed simulations using a predator-prey

model to explore in which conditions a "predation-release" effect could increase the abundance of small prey species (see Appendix 3 for detailed methods). We found that small to intermediate disturbance regimes can increase average prey abundance through a "predation-release" effect, which should generate size-abundance pyramids with a wider base (Fig. 6c). This effect vanishes above some disturbance thresholds, where prey species are also negatively impacted by disturbances (Fig. 6c and Figs. S9-S11).

Our model cannot capture cascading effects triggered by complex interactions networks in its current form. A promising future direction is the extension of the model to multitrophic communities, which will allow further explorations of the potential of interspecific interactions to modulate the impact of disturbances on size-abundance pyramids and community biomass. Indeed, it is likely that predator species will also be impacted indirectly through a bottom-up transmission of the disturbances (i.e. decrease in prey availability).

Additional mechanisms shaping size-abundance pyramids exposed to disturbances

Here, we propose a systematic approach, based on the metabolic theory of ecology, to predict the response of size-abundance pyramids to persistent disturbances. Our results are specific to a class of persistent disturbances (i.e. pulse or press) that affect the abundance of all species in a similar way, regardless of their specific body-size or growth rate. We also assume that the leading mechanism that determines the response of size-abundance pyramids to this type of disturbances is the allometric relationship between growth rates and body-size. However, additional mechanisms can generate size-dependent abundances or size-dependent responses to disturbances in real world ecosystems. First, species sensitivity to disturbances that are not size-selective can be nonetheless unequal among size classes, with particular size-classes being more resistant to a given disturbance intensity. For example, large tree species are more resistant to drought compared to

small ones with shallower roots (REF, to double check if it is true!). Conversely, small tree species are less impacted by strong winds or hurricanes compared to large ones (REFS). From a spatial perspective, size-specific mobility and immigration-extinction dynamics could largely affect the relationship between species recovery dynamics and their size (McCann *et al.* 2005). It would be interesting to extend our approach to metacommunities, where the depletion of large species in a disturbed habitat patch could be balanced by immigration from undisturbed neighboring patches (Pawar 2015).

Finally, some disturbances can be size-selective, as illustrated by studies on abundance size spectra that specifically addressed the effect of a press, size-selective disturbance, often reflecting disturbances expected under commercial fishing (Shin et al. 2005; Sprules & Barth 2016). Our model can easily be refined to more specific cases, in which disturbances have unequal effects on species, by adding size-specific disturbance intensities to the model. The abundance size spectra of harvested fish communities are generally characterized by steeper slopes than unfished communities, and are used as a size-based indicator of fisheries exploitation (Shin *et al.* 2005; Petchey & Belgrano 2010; Sprules & Barth 2016). We demonstrate that size-abundance pyramids are also predictably affected by more general pulse disturbances that are not size-selective such as floods or wildfires. Hence, when compared to a reference state, size-abundance pyramids provide information on the level of disturbances an ecosystem is facing and could be used as "universal indicators of ecological status", as advocated in Petchey & Belgrano (2010)

Conclusion

Our findings have direct implications regarding the effects of disturbances on ecosystem functioning. Indeed, the model makes predictions on total biomass and demographic traits correlated to productivity rate and energy flows, which are among the most relevant metrics to

quantify ecosystem functioning (Oliver *et al.* 2015; Schramski *et al.* 2015; Brose *et al.* 2016; Barnes *et al.* 2018). In the current context of global change, we demonstrate that the expected increase in disturbance frequency and intensity should accelerate the extinction of the largest species, leading to an increasing proportion of communities dominated by small, fast-growing species and lower levels of standing biomass. Importantly, the effect of increasing disturbance regimes will be nonlinear and abrupt changes in community structure and functioning are expected once a disturbance threshold affecting the equilibrium abundances of smaller species is reached.

DATA AVAILABILITY STATEMENT

The data supporting the experimental results will be archived in the Dryad Digital Repository. We will release the code through a Rmarkdown document, and an associated C++ source code file, which explains in detail the theoretical approach and produces the theoretical figures. A doi will be provided after acceptance. The provided html file shows the output of the Rmarkdown document.

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539

FIGURE LEGENDS

Figure 1: A trophic pyramid (a) describes the distribution of biomass along discrete trophic levels, and assumes that all species within a trophic level have the same functional traits. The community size-structure (b) and the size-abundance pyramid (c) are equivalent size-centric representations of ecological communities and are the focus of this study. They describe the distribution of abundance across body-sizes and can studied both within and across trophic levels. b) the community size-structure depicts log(body-size) on the x-axis and log(abundance) on the y-axis, while c) the size-abundance pyramid shows log(abundance) on the x-axis and log(body-size) on the y-axis. Note that the area A is the same in both panels. We use the community size-structure representation throughout the paper as it facilitates comparisons between theory and experimental data, but see Fig. 6 for a synthesis of our findings using the pyramid representation.

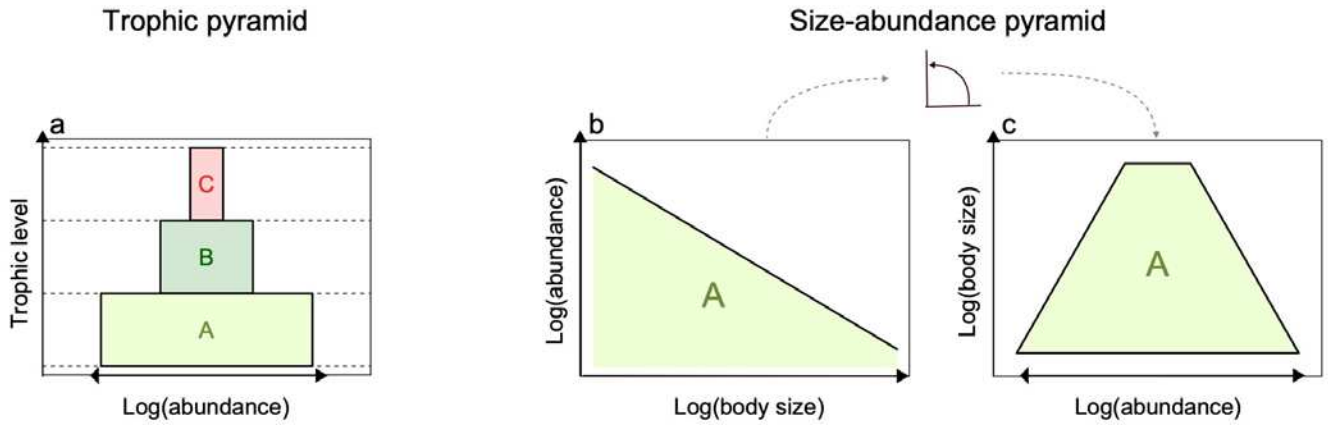
Figure 2: Population dynamics and persistence according to disturbance regime. a) Temporal dynamics of two species experiencing the same disturbance regime. Species 1 has a smaller body-size and therefore a higher growth rate than species 2. A population can persist only if its growth rate balances the long-term effect of the disturbance regime. We derive in equation (4) the mean abundance at dynamical equilibrium (i.e. temporal mean) of the persisting species experiencing varying disturbance regimes. b) Isoclines of the persistence criterion in the disturbance regime landscape according to population growth rate (numbers): on and above the line, the population of a given growth rate goes extinct. Lines with the same color code as in panel (a) correspond to the same growth rate.

Figure 3: Effects of disturbance frequency and intensity on community size-structure and average total biomass at dynamical steady state. Analytical results derived from Equation (5). a) Effect of

564 disturbance frequency (disturbance intensity is fixed to 50% abundance reduction), and b)
565 disturbance intensity (disturbance frequency is fixed to 0.25) on community size-structure. c)
566 Effect of disturbance frequency and d) intensity on average total biomass (in log), for different
567 intensities (c) and frequencies (d), respectively. Points on the black lines in (c) and (d) show the
568 disturbance regimes corresponding to community size-structures of the respective colors displayed
569 in panels (a) and (b).
570
571 **Figure 4:** Experimental results. a) Effect of disturbance frequency on community size-structure.
572 Vertical bars illustrate mean abundance (individuals/µl) and its standard deviation over 21 time
573 points and 6 replicates for each size-class (μm^2). Disturbance intensity is fixed to $I = 90\%$; other
574 intensities are shown in Fig. S2 and statistics in Table S2. b) Effect of disturbance intensity on
575 community size-structure. Disturbance frequency is fixed to $f = 0.33$, other frequencies are
576 shown in Fig. S3 and statistics in Table S2. Controls are in grey (undisturbed environment) and
577 axes are on a logarithmic scale. c) Effect of disturbance frequency on total community biomass
578 (temporal mean, n = 6 for treatments, n = 8 for controls, in $\mu m^2/\mu l$). Disturbance intensity is fixed
579 to $I = 90\%$ as in panel (a); other intensities are shown in Fig. S2. All frequencies have a
580 significant negative effect on total biomass compared to controls: Welch two sample t-tests: $f_{0.08}$:
581 t = 8, p-value < 0.001, $f_{0.11}$: t = 8.5, p-value < 0.001, $f_{0.16}$: t = 13.2, p-value < 0.001, $f_{0.33}$: t = 14.2,
582 p-value < 0.001. d) Effect of disturbance intensity on total community biomass (temporal mean, n
583 = 6 for treatments, n = 8 for controls, in $\mu m^2/\mu l$). Disturbance frequency is fixed to $f = 0.33$ as in
584 panel (b); other frequencies are shown in Fig. S3. All intensities except $I = 10\%$ and 30% have a
585 significant negative effect on total biomass compared to controls: $I_{10\%}$: t = 0.75, p-value = 0.48,

586 $I_{30\%}$: t = 0.5, p-value = 0.63, $I_{50\%}$: t = 6.1, p-value < 0.001, $I_{70\%}$: t = 12.7, p-value < 0.001, $I_{90\%}$: t =
587 14.2, p-value < 0.001.
588
589 **Figure 5: Comparison between experimental results and model predictions.** a) Predicted vs.
590 observed mean abundance *N* relative to carrying capacity *K* in the twelve size-classes for all the
591 disturbance regimes (n=240). Solid line: linear regression [y = -0.04 + 0.96x, R^2 = 0.96, p-value
592 < 0.001. Standard error for slope: 0.01, intercept: 0.03]. Dashed line indicates a 1:1 relationship.
593 b) Predicted effect of disturbance frequency on the community size-structure of experimental
594 communities. Disturbance intensity is fixed to *I* = 90%; other disturbance regimes are shown in
595 Figs. S4-S5. Controls are in black (undisturbed environment) and axes are on a logarithmic scale.
596 c) Observed effect of disturbance frequency on the community size-structure of experimental
597 communities (similar to Fig. 4a). d) Relative difference between observed and predicted mean
598 abundance for each size-class, i.e. $(N_{obs} - N_{pred})/ N_{pred}$.
599
600 **Figure 6: Graphical summary of the effects of disturbances on the shape of size-abundance**
601 **pyramids.** Panels (a) and (b) show size-abundance pyramids for increasing disturbance frequency
602 and intensity, respectively (same analytical results as in Fig. 3a-b). Panel (c) illustrates the expected
603 change in the shape of size-abundance pyramids resulting from a predator-prey dynamic. Lines and
604 points in panel (c) represent isoclines of disturbance regimes {*I*, *T*} under which we can expect a
605 predation-release effect leading to wider bases of size-abundance pyramids. Points represent the
606 disturbance intensity for which prey species switch from higher to lower mean abundances at
607 dynamical equilibrium in presence compared to in absence of disturbances, for a given disturbance
608 frequency and a set of predator parameters. Black points are estimated for a smaller prey, i.e. with
609 higher growth rate, than grey points (see detailed method in Appendix 3 and Table S4 for parameter

values).



611

612 **Figure 1**.

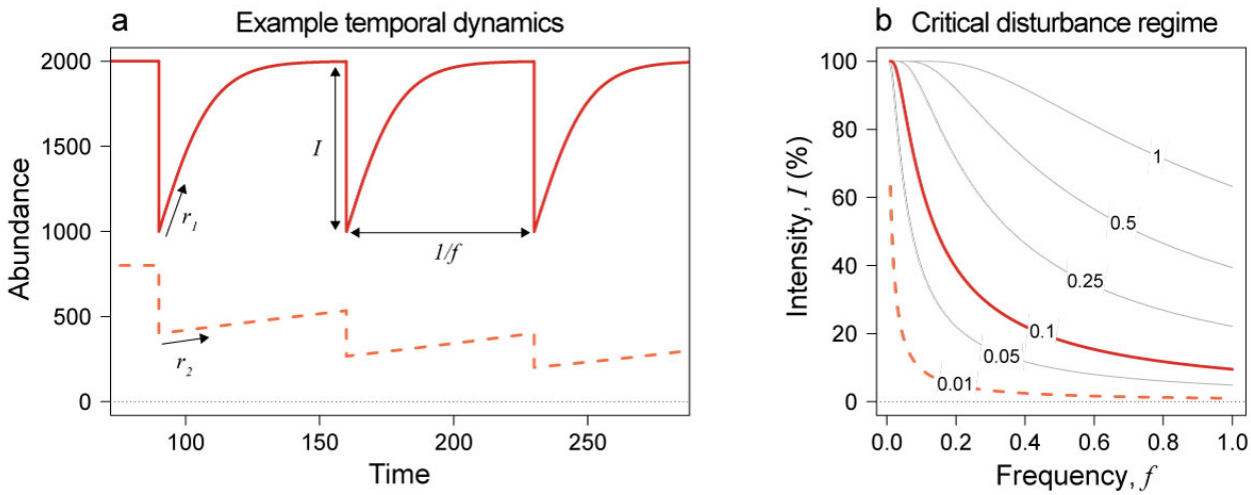
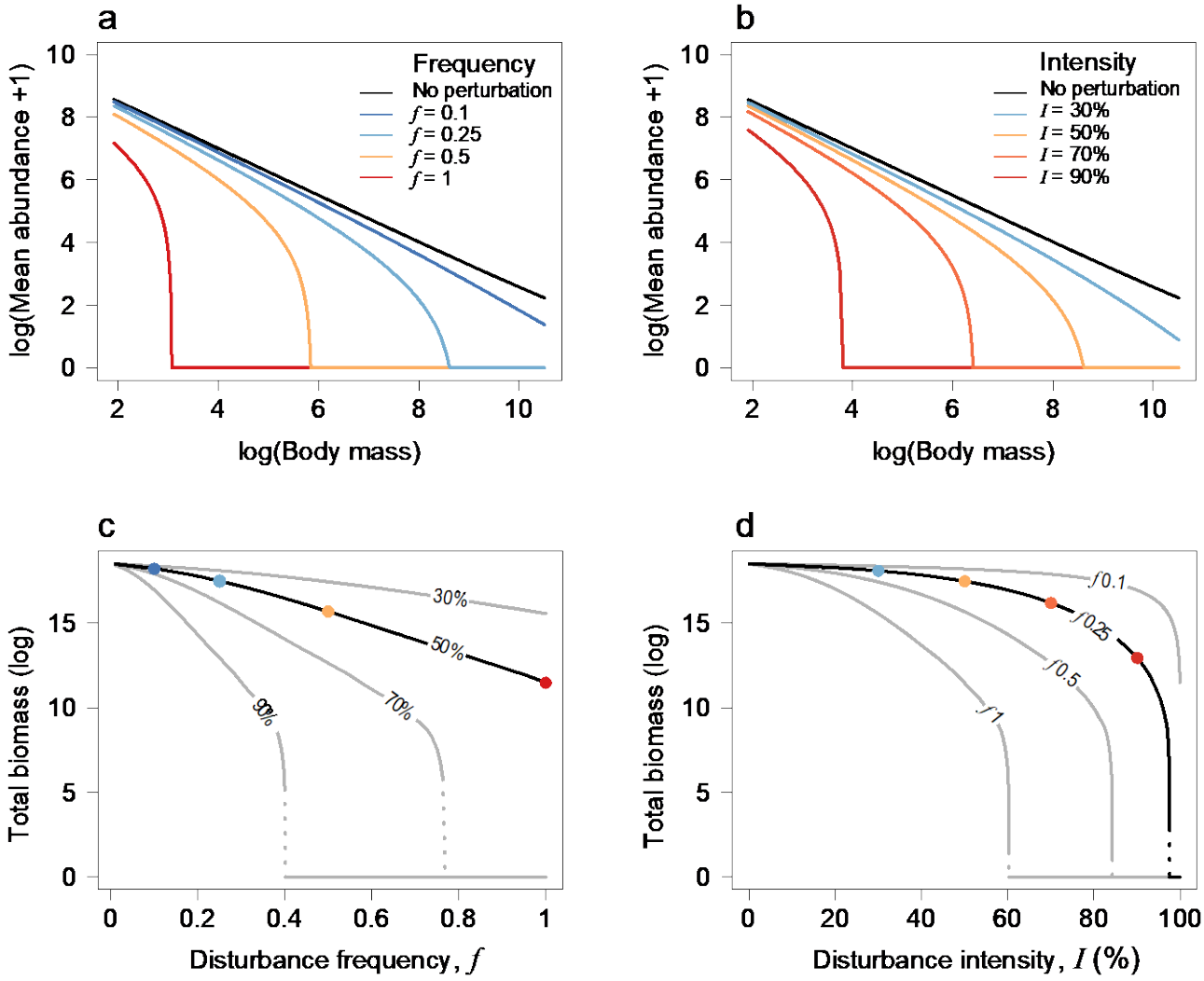

a
Example temporal dynamics
Abundance
Time
I
1/f
r1
r2
b
Critical disturbance regime
Intensity, I (%)
Frequency, f
1
0.5
0.25
0.1
0.05
0.01

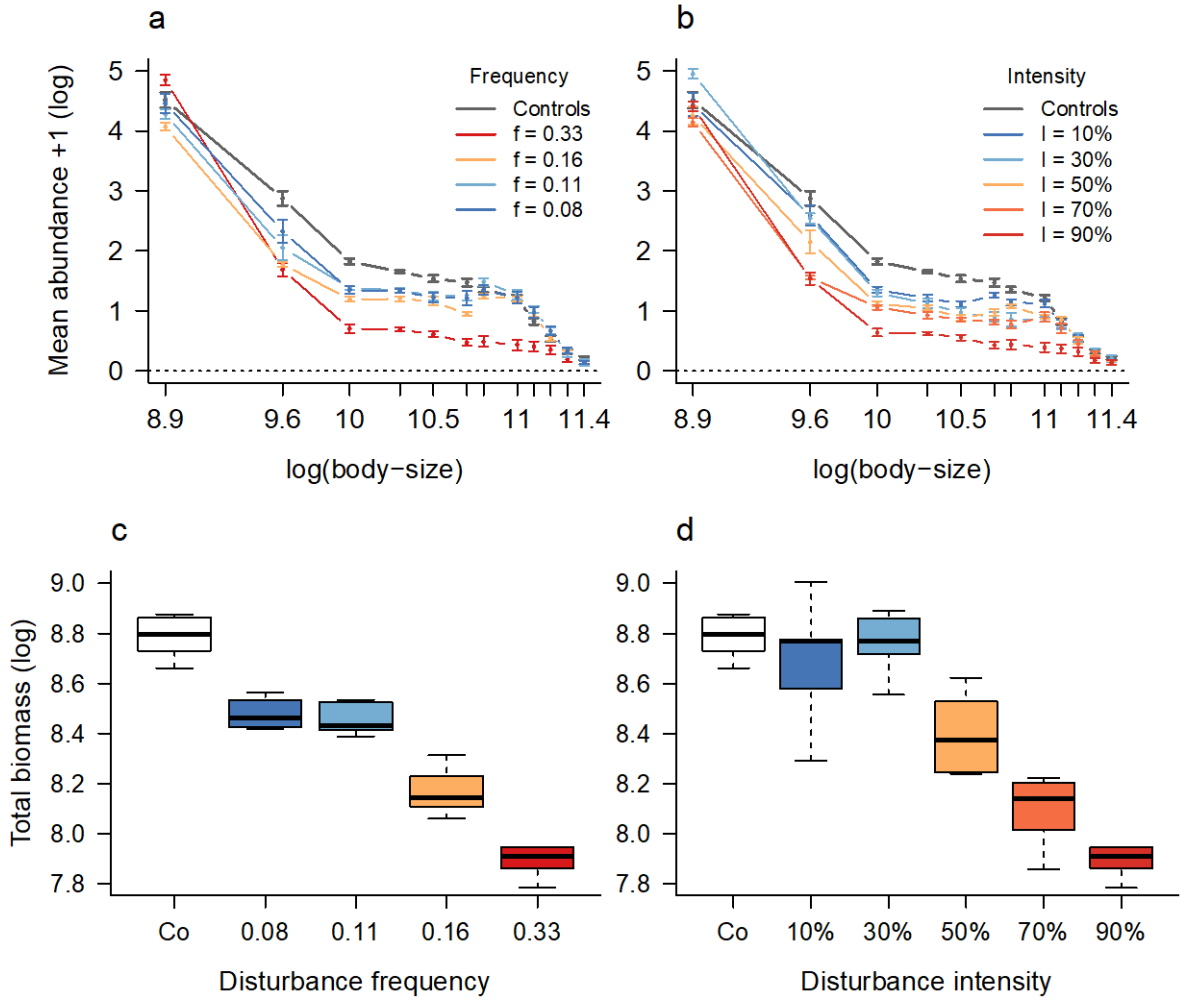
Figure 2.

615



616

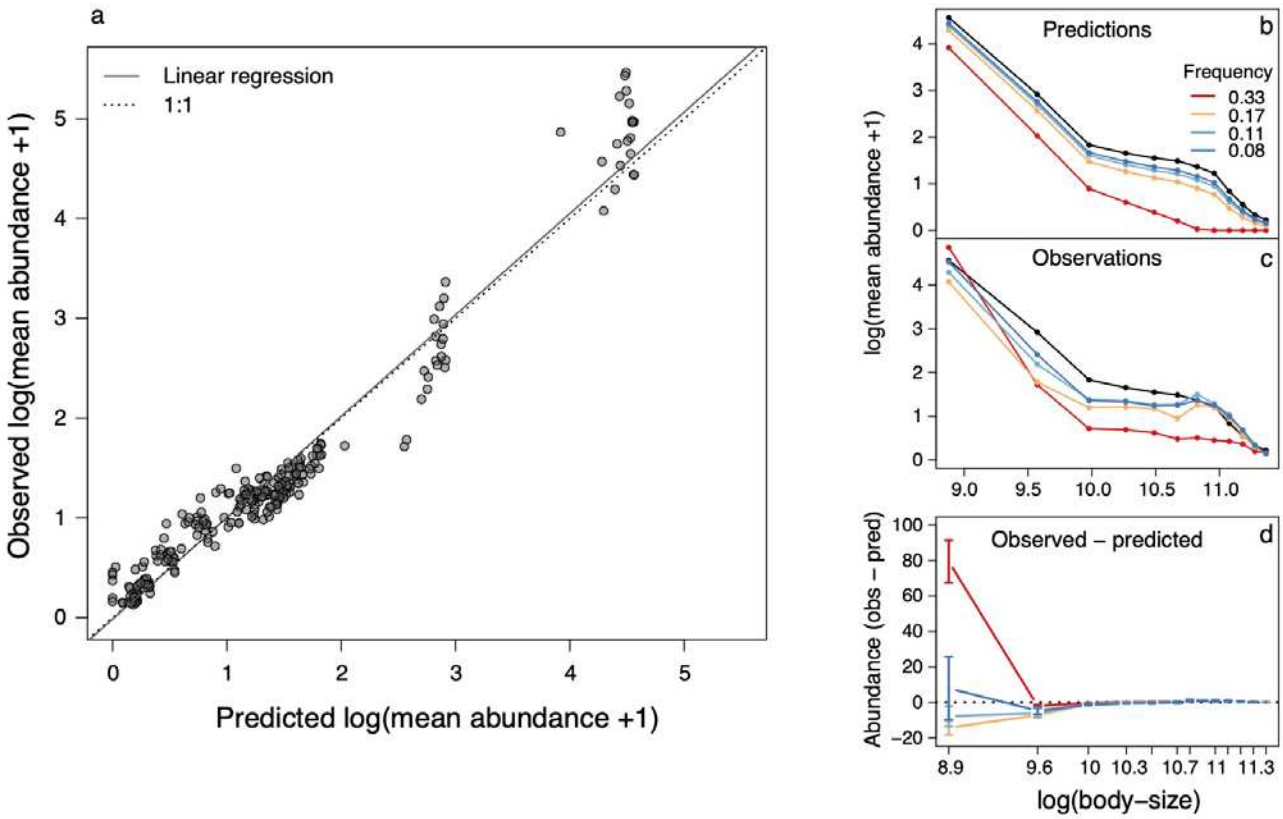
617 **Figure 3.**



618

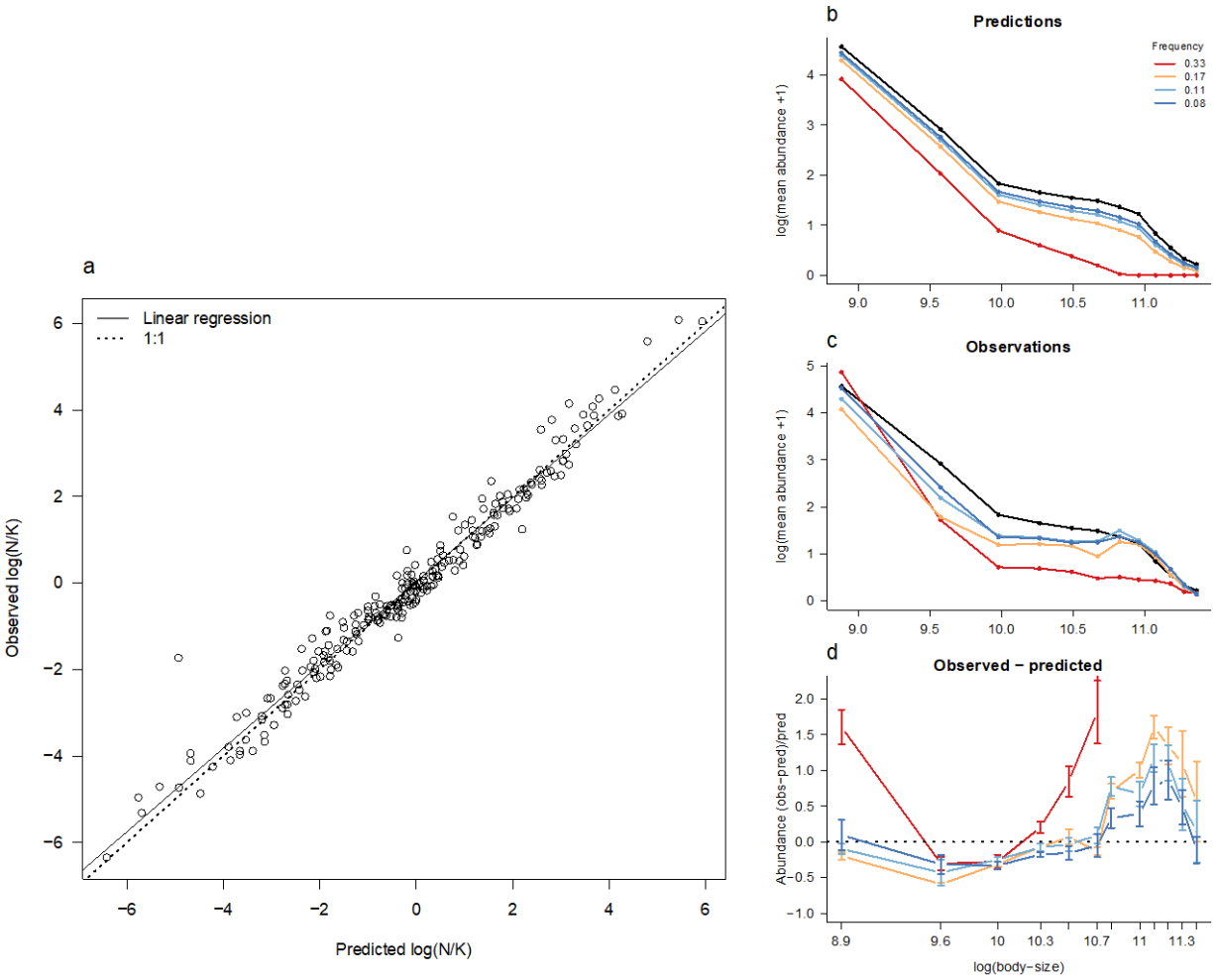
619 **Figure 4**.

620


a
Linear regression
1:1
Observed log(mean abundance +1)
Predicted log(mean abundance +1)
b
Predictions
Frequency
0.33
0.17
0.11
0.08
c
Observations
log(mean abundance +1)
d
Observed – predicted
Abundance (obs – pred)
log(body–size)

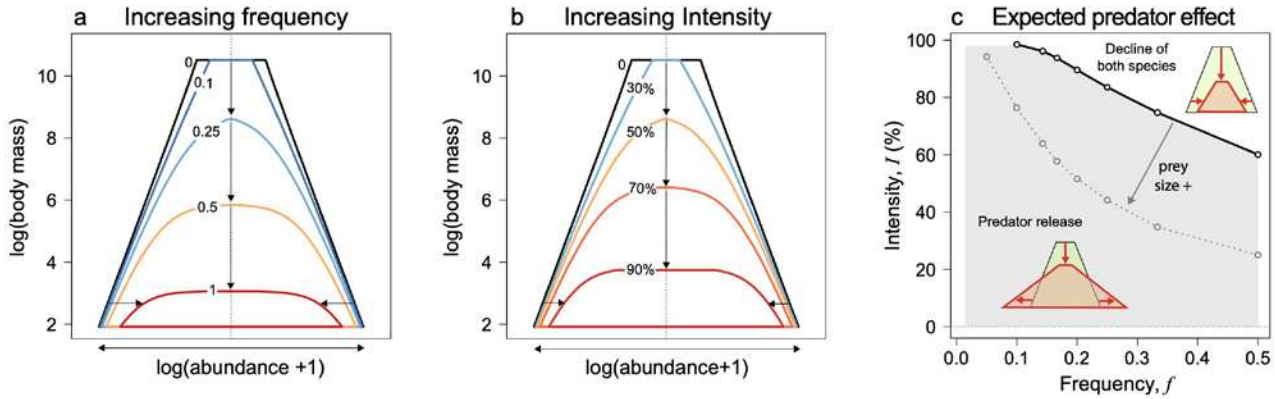
621

622



623

624 **New Figure 5.**



625

626 **Figure 6.**